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Benjamin J. Rook , Michael J. Hansen & Owen T. Gorman

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Benjamin J. Rook*

Cramer Fish Sciences, 13300 New Airport Road, Auburn, California 95602, USA

Michael J. Hansen

U.S. Geological Survey, Hammond Bay Biological Station, 11188 Ray Road, Millersburg, Michigan 49759, USA

Owen T. Gorman

U.S. Geological Survey, Lake Superior Biological Station, 2800 Lake Shore Drive East, Ashland, Wisconsin 54806, USA

Abstract

The cisco *Coregonus artedi* was once the most abundant fish species in the Great Lakes, but currently cisco populations are greatly reduced and management agencies are attempting to restore the species throughout the basin. To increase understanding of the spatial scale at which density-independent and density-dependent factors influence cisco recruitment dynamics in the Great Lakes, we used a Ricker stock–recruitment model to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. We found that the recruitment variation of ciscoes in Lake Superior was best described by a five-parameter regional model with separate stock–recruitment relationships for the western, southern, eastern, and northern regions. The spatial scale for modeling was about 260 km (range = 230–290 km). We also found that the density-independent recruitment rate and the rate of compensatory density dependence varied among regions at different rates. The density-independent recruitment rate was constant among regions (3.6 age-1 recruits/spawner), whereas the rate of compensatory density dependence varied 16-fold among regions (range = −0.2 to −2.9/spawner). Finally, we found that peak recruitment and the spawning stock size that produced peak recruitment varied among regions. Both peak recruitment (0.5–7.1 age-1 recruits/ha) and the spawning stock size that produced peak recruitment (0.3–5.3 spawners/ha) varied 16-fold among regions. Our findings support the hypothesis that the factors driving cisco recruitment operate within four different regions of Lake Superior, suggest that large-scale abiotic factors are more important than small-scale biotic factors in influencing cisco recruitment, and suggest that fishery managers throughout Lake Superior and the entire Great Lakes basin should address cisco restoration and management efforts on a regional scale in each lake.

The cisco *Coregonus artedi* is a pelagic fish species endemic to North America (Scott and Crossman 1973; Lee et al. 1980; Becker 1983). A member of the family Salmonidae and the subfamily Coregoninae, typical individuals are elongate and silver with a black, blue-green, gray, or tan back (Scott and Crossman 1973; Becker 1983). The species averages 203–305 mm total length (TL; Scott and Crossman 1973) and 75–285 g in weight (Scott and Crossman 1973; Fisher and Fielder 1998). Native

and introduced populations inhabit water bodies from the Great Lakes and upper Mississippi River drainage throughout eastern and central Canada (Lee et al. 1980; Becker 1983; Fisher and Fielder 1998). Near the northern limit of the species range, individuals inhabit large rivers, ponds, and coastal waters of Hudson Bay (Scott and Crossman 1973; Lee et al. 1980; Becker 1983). In the Great Lakes region, the cisco is limited to oligotrophic and mesotrophic lakes (Scott and Crossman 1973; Becker 1983;

Latta 1995; Edsall and DeSorcie 2002), where it serves as a highly efficient trophic intermediary linking crustacean zooplankton production to native piscivore and benthivore stocks through predation (Dryer and Beil 1964; Dryer et al. 1965; Conner et al. 1993; Edsall and DeSorcie 2002; Bronte et al. 2003; Hoff 2004; Schram et al. 2006; Ray et al. 2007; Gorman and Hoff 2009) and mass egg deposition during autumn spawning (Anderson and Smith 1971; Scott and Crossman 1973; Becker 1983).

Historically, the cisco was the most abundant and most ecologically and economically important fish species in the Great Lakes (Smith 1995). However, by the mid-1900s, cisco populations were greatly reduced throughout the basin (Berst and Spangler 1973; Christie 1973; Hartman 1973; Lawrie and Rahrer 1973; Wells and McLain 1973). Similar to other native fishes (Christie 1974), overfishing, habitat degradation, and interactions with exotic species caused cisco yield to decline by 80–99% in each lake (Baldwin et al. 2006). Declining yields brought about new regulations designed to prevent further losses, but except for a few remnant populations (Mills et al. 2005; Mohr and Ebener 2005; Stockwell et al. 2009), cisco stocks failed to recover in the lower Great Lakes. Reduced commercial fishing pressure enabled ciscoes to recover in portions of Lake Superior, but historical stock structure was altered (Goodyear et al. 1981; Selgeby 1982; Horns 2003); abundance is now driven by highly erratic age-1 recruitment and few year-classes of adults (Bronte et al. 2003; Hoff 2004; Gorman and Hoff 2009). Because of the historical ecological importance of the species (Smith 1995) and recent declines in other forage fishes, such as the alewife *Alosa pseudoharengus*, throughout the lower Great Lakes (O'Gorman and Stewart 1999), management agencies have begun exploring the feasibility of restoring cisco stocks throughout Lake Superior and the entire Great Lakes basin. However, limited understanding of factors that drive recruitment variation and the spatial scale at which these factors operate have led researchers to question the long-term sustainability and restoration potential of the species (Hoff 2004; Fitzsimons and O'Gorman 2006; Ebener et al. 2008; Stockwell et al. 2009; Zimmerman and Krueger 2009). A comprehensive analysis of cisco stock–recruitment in Lake Superior can provide a framework for addressing these questions.

The stock–recruitment relationship quantifies the ability of a fish stock to replace itself over a range of spawning stock sizes (Koslow 1991; Hilborn and Walters 1992), and is essential to many models used to estimate optimal fishing strategies (Koslow 1991). However, the stock–recruitment relationship is often obscured by the effects of environmental variation, and in some cases inadequate population measures, thereby causing recruitment to appear independent of spawning stock size (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). Recruitment can be indexed at any life stage, but for many fish stocks, recruitment is established within the first year of life, primarily during egg and larval stages (Ricker 1975). Spawning stock size and environmental variation collectively determine egg and lar-

val survival through density-dependent and density-independent mechanisms (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). When annual variation in recruitment is driven by environmental variables, multifactor stock–recruitment models can be used to quantify the separate effects of environmental variation and spawning stock size on recruitment (Ricker 1975; Walters et al. 1986; Madenjian et al. 1996; Hansen et al. 1998; Hoff 2004). Identifying the appropriate spatial scale for modeling the stock–recruitment relationship is an important preliminary step in any multifactor stock–recruitment analysis.

The U.S. Geological Survey (USGS, Lake Superior Biological Station, Ashland, Wisconsin) has conducted spring bottom-trawl surveys of the nearshore fish community in U.S. waters of Lake Superior since 1978 and Canadian waters of Lake Superior since 1989. During 1978–2007, age-1 cisco recruitment varied 339-fold in U.S. waters (1978–2007) and 48-fold in Canadian waters (1989–2007; USGS, Lake Superior Biological Station, Ashland, Wisconsin). Strong recruitment events were highly synchronous across the lake (Kinnunen 1997; Bronte et al. 2003; Ebener et al. 2008; Gorman and Hoff 2009; Stockwell et al. 2009) and characterized by large regional differences in year-class strength. Lakewide recruitment events occurred in 1984, 1988–1990, 1998, and 2003 (Ebener et al. 2008; Stockwell et al. 2009). Additional localized, large year-classes were established in Minnesota waters in 1978 and eastern Michigan waters in 1983. In 1984, the large year-class in Minnesota waters was smaller than in other U.S. waters (Stockwell et al. 2009). In 1998, the large year-class in eastern Michigan and eastern Ontario waters was smaller than in other U.S. and Canadian waters (Ebener et al. 2008; Stockwell et al. 2009). Large regional differences in age-1 cisco year-class strength and regional deviations from normal patterns of recruitment synchrony suggest that separate stock–recruitment models should be developed for western, southern, eastern, and northern regions of Lake Superior (e.g., spatial scales >200 km). Previous studies using otolith microchemistry and parasites as markers of cisco stock structure in Lake Superior generally support the regional spatial scale for modeling (Bronte et al. 1996; Hoff et al. 1997b). However, previous studies of commercial fishery records and cisco genetics suggest the presence of at least six to eight spatially discrete cisco spawning stocks in Wisconsin waters of Lake Superior (Goodyear et al. 1981; Selgeby 1982) and two genetically discrete stocks in Black Bay and Thunder Bay (K. T. Scribner, Michigan State University, personal communication). Similarly, a tagging study of ciscoes in Lake Michigan reported that nearly all fish were recaptured within about 40 km of their initial tagging site (Smith and Van Oosten 1940). Therefore, models targeting spatially or genetically discrete cisco spawning stocks should be developed for much smaller spatial scales (e.g., <40–60 km).

Our objective was to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. Because some of the weakest cisco year-classes are generally produced by large parental stocks, whereas some of

the strongest cisco year-classes are produced by small parental stocks (Bronte et al. 2003; Horns 2003; Hoff 2004; Gorman and Hoff 2009), we therefore used a Ricker stock–recruitment model (Ricker 1975) to identify and quantify the appropriate spatial scale for modeling. We expected to find that multiple spatial units (described below) within geographic regions could be modeled using a single set of stock–recruitment parameters because large-scale abiotic factors are generally considered more important than small-scale biotic factors in driving age-1 cisco recruitment in Lake Superior (Kinnunen 1997; Bronte et al. 2003; Hoff 2004; Gorman and Hoff 2009; Stockwell et al. 2009). We also expected to find compensatory density dependence for regional stock–recruitment models because Hoff (2004) found significant compensatory density dependence in Wisconsin waters of Lake Superior. Finally, we expected to find different rates of compensatory density dependence among regional stock–recruitment models because age-1 cisco recruitment varies regionally in Lake Superior (Ebener et al. 2008; Stockwell et al. 2009).

METHODS

Study area.—Lake Superior is located near the head of the St. Lawrence River drainage and is bordered on the north by Ontario and on the south by Michigan, Wisconsin, and Minnesota (Figure 1). A surface area of 8.24×10^6 ha and a volume of 12,233 km^3 make Lake Superior the largest of the Great Lakes (Lawrie and Rahrer 1973). Lake Superior is highly oligotrophic (Hansen 1990). Primary production is near the low end of the range for freshwater lakes, so commercial fish production per unit of surface area is lower than in all other Great Lakes (Hansen 1990; Horns 2003). The native fish community of Lake Superior included 73 species in 18 families (Lawrie 1978), but biomass was dominated by lake trout *Salvelinus namaycush*, lake whitefish *Coregonus clupeaformis*, cisco, and several species of related deepwater ciscoes of the genus *Coregonus* (Hansen 1990). Lake Superior has been little affected by point or nonpoint source pollution. The greatest influences from human development have been overfishing and introductions of exotic species, especially the sea lamprey *Petromyzon marinus* (Lawrie and Rahrer 1973; Hansen 1990).

Cisco sampling.—Cisco recruitment was indexed using catch rates of age-1 ciscoes in spring bottom-trawl surveys when fish were 13–14 months of age and 140 mm TL or less (Hoff 2004). Large cisco year-classes typically include a significant number of individuals greater than 140 mm TL (USGS, Lake Superior Biological Station, Ashland, Wisconsin), so length-frequency distributions were examined and the TL cut-off was adjusted to include all age-1 individuals. Spring bottom-trawl surveys of the Lake Superior nearshore fish community included an average of 49 sites (range = 32–53) in U.S. waters since 1978 and an average of 30 sites (range = 18–34) in Canadian waters since 1989 (Figure 1).
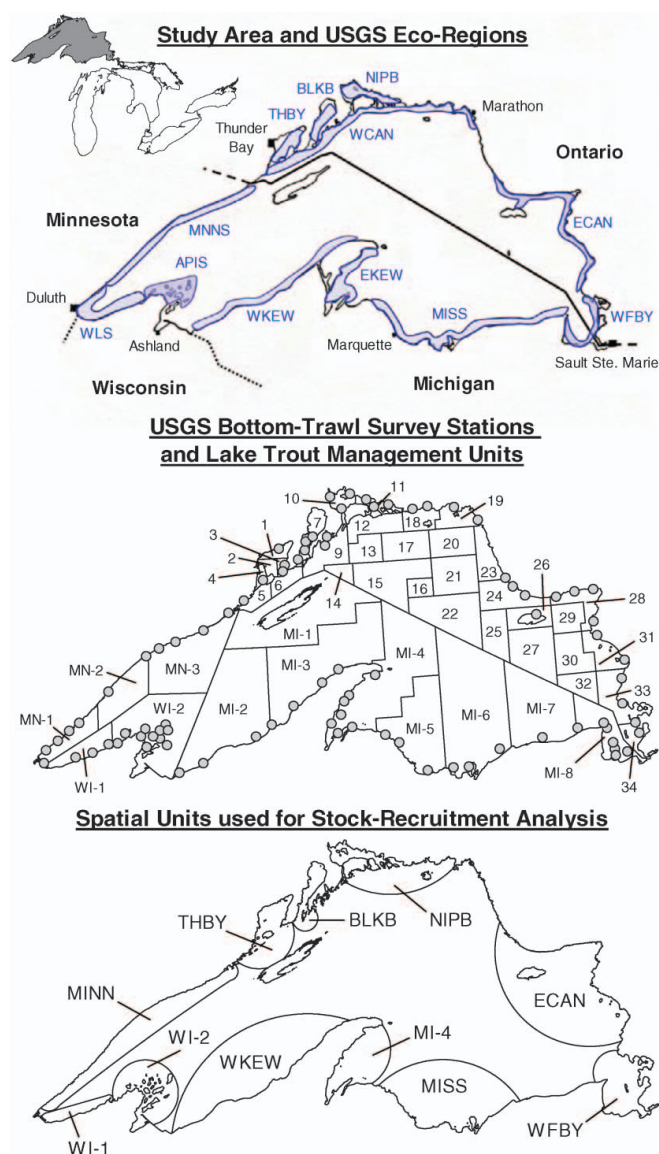

FIGURE 1. Study area and locations of: (1) U.S. Geological Survey (USGS) Eco-Regions (Gorman and Todd 2007), (2) U.S. Geological Survey spring bottom-trawl survey stations (points) and lake trout management units (polygons; Hansen 1996), and (3) spatial units used for stock–recruitment analysis. Eco-Regions were developed to provide more meaningful regional analyses of Lake Superior aquatic communities than politically based management units and are based on observed changes in habitat (MNNS = Minnesota North Shore, WLS = Western Lake Superior, APIS = Apostle Islands, WKEW = Western Keweenaw, EKEW = Eastern Keweenaw, MISS = Michigan South Shore, WFBY = Whitefish Bay, ECAN = Eastern Canada, WCAN = Western Canada, NIPB = Nipigon Bay, BLKB = Black Bay, and THBY = Thunder Bay; see Gorman and Todd 2007 for a more complete description). Lake trout management units in U.S. waters are denoted by a unique alpha-numeric code (MI = Michigan, WI = Wisconsin, and MN = Minnesota) and jurisdictions in Canadian waters are denoted by a unique numeric code (Hansen 1996). For spatial units, MINN = Minnesota, WI-1 = lake trout management unit WI-1, WI-2 = lake trout management unit WI-2, WKEW = Western Keweenaw, MI-4 = lake trout management unit MI-4, MISS = Michigan South Shore, WFBY = Whitefish Bay, ECAN = Eastern Canada, NIPB = Nipigon Bay, BLKB = Black Bay, and THBY = Thunder Bay. [Figure available in color online.]

Yankee bottom-trawls (3/4) with an 11.9-m headrope, 15.5-m footrope, 2.2-m wing height, 89- and 64-mm stretch mesh, and a 13-mm mesh cod end were towed at a speed of 3.5 km/h across contours at fixed sampling stations spaced about 24 km apart along the U.S. and Canadian shorelines. Trawling began at a depth of 10–15 m and progressed in an offshore direction until 60 min elapsed or the trawl reached the maximum depth for that area of the nearshore zone. Trawling targeted all fish species and was conducted during daylight hours. Catches from each trawl tow were grouped by species and individual fish were measured for TL (mm). Density (fish/ha) was computed from the total number of fish caught and the area swept by each trawl tow. Data were summarized for each trawl tow (USGS, Lake Superior Biological Station, Ashland, Wisconsin).

Cisco spawning stock size was indexed using catch rates of adult cisco in bottom-trawls in U.S. and Canadian waters (described above), fishery-independent gill-net surveys in U.S. waters, and targeted commercial fisheries in Canadian waters. Most agencies with jurisdiction in Lake Superior conducted fishery-independent summer lake trout surveys with graded-mesh, bottom-set gill nets placed at fixed sampling stations throughout lake trout management units (Hansen 1996; Figure 1). Although most surveys did not target cisco, the species was collected as bycatch (Ebener et al. 2008). Summer surveys were conducted in all Wisconsin lake trout management units beginning in 1970 and since the mid-1980s in all Minnesota and most Michigan lake trout management units. The average depth of summer survey nets was 34 m in Wisconsin (range = 18–61 m), 45 m in Minnesota (range = 36–57 m), and 46 m in Michigan (range = 15–105 m; Ebener et al. 2008). Soak times typically ranged 1–4 nights. Catch per unit effort (CPUE; fish/km) was computed from the number of fish caught and net length. Data were summarized by mesh size and species for each gill-net gang. Before analysis, data were standardized to a soak time of one night by dividing by total number of nights. Fishery-independent gill-net surveys were not available for Canadian lake trout management units (Ebener et al. 2008), so CPUE in targeted commercial fisheries was used to index cisco spawning stock size. During 1967–1975, the commercial cisco fishery in Ontario was primarily a flesh fishery and relied on trawling. However, by the early-1980s, the fishery had transitioned to a roe fishery and relied on floating gill-nets targeting gravid adult females during autumn spawning (Dextrase et al. 1986). Commercial operators reported daily total biomass (kg) of ciscoes harvested, effort (km), and locations of harvest. Catch per unit effort (kg/km) was computed from biomass caught and net length for each gill-net gang in each lake trout management unit (Yule et al. 2006).

In Lake Superior, most ciscoes are classified as mature at 200 mm TL in spring (Hoff 2004) and 250 mm TL in autumn (Dryer and Beil 1964; Yule et al. 2006). Therefore, cisco spawning stock size was indexed as the density of fish 200 mm TL or longer in spring bottom-trawl surveys, CPUE of fish 225 mm TL or longer in summer lake trout surveys, and CPUE

of fish 250 mm TL or longer in autumn commercial fisheries. Total length cutoffs were applied to density distribution data from spring bottom-trawl surveys to calculate the density of fish 200 mm TL or longer. Mesh sizes used in summer lake trout surveys varied among agencies, so only mesh sizes from 2.0- to 2.5-in (51- to 64-mm) stretch-measure were used to index cisco spawning stock CPUE. Based on a preliminary analysis of length-frequency distributions for various mesh sizes, this mesh-size range probably excludes smaller and larger adult ciscoes but is the most appropriate standardized index of cisco spawning stock size ($\geq$225 mm TL) in summer. Because mesh sizes used in the Ontario commercial fishery were generally 3.0- to 3.5-in (76- to 90-mm) stretch-measure (Dextrase et al. 1986; Stockwell et al. 2009) and the fishery targeted spawning fish (Dextrase et al. 1986), we assumed that commercial CPUE appropriately indexed cisco spawning stock size ($\geq$250 mm TL) in autumn.

Spatial summarization.— We defined 11 spatial units in U.S. and Canadian waters of Lake Superior (Figure 1) and calculated summary statistics for each index of recruitment and spawning stock size in each spatial unit. Spatial units were required to account for different spatial scales used for data collection and reporting and were based on regional combinations of whole (U.S. and Canadian waters) and partial (Canadian waters) lake trout management units (described above) that loosely corresponded to U.S. Geological Survey Eco-Regions (Gorman and Todd 2007; Figure 1). For bottom-trawl density and fishery-independent gill-net CPUE, individual observations were treated as replicate samples and used to calculate summary statistics for each spatial unit. For targeted commercial fishery CPUE, individual observations were treated as replicate samples and used to calculate summary statistics for each whole and partial lake trout management unit. Weighted averages for whole and partial lake trout management units were then used to calculate summary statistics for each spatial unit. Weights were based on the area of each whole and partial lake trout management unit. In two Canadian lake trout management units, the availability of targeted commercial fishery CPUE was erratic but was strongly and linearly related to the CPUE from a neighboring unit. Therefore, prior to calculating summary statistics for each spatial unit, linear regression (Zar 1999) was used to predict CPUE for lake trout management units in which targeted commercial fishery CPUE was not available.

Model description, selection, and validation.—To identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior, estimates of spawner density were paired with estimates of recruit density 2 years later, and a sequence of Ricker stock–recruitment models (Ricker 1975) were fitted to describe varying spatial scales for age-1 cisco recruitment dynamics. The Ricker stock–recruitment model describes recruitment of the i th year-class (R_i) as a function of spawning stock size (S_i; Ricker 1975), i.e.,

$$R_i = \alpha S_i e^{-\beta S_i} e^\varepsilon,$$

where α is the number of recruits produced per spawner at low spawning stock size, β is the rate at which the logarithm of recruits per spawner declines with spawning stock size, and $e^{\varepsilon} =$ multiplicative process error (Ricker 1975). Stock–recruitment errors are usually lognormal (Peterman 1981), so parameters (α and β) were estimated using linear regression (Zar 1999) and the additive-error $\log_e$-transformed model

$$\log_e(R_i/S_i) = \log_e(\alpha) - \beta S_i + \varepsilon.$$

Stock–recruit density estimates were used to fit stock–recruitment curves at five different spatial scales in Lake Superior. A priori spatial models included: (1) a 22-parameter global model (model 1) where a separate stock–recruitment curve was fit to density estimates for each of 11 spatial units, (2) a two-parameter reduced model (model 2) where one stock–recruitment curve was fit to density estimates for the entire lake, (3) a six-parameter regional model (model 3) where separate stock–recruitment curves were fit to density estimates for western, eastern, and northern spatial units, (4) an eight-parameter regional model (model 4) where separate stock–recruitment curves were fit to density estimates for western, southern, eastern, and northern spatial units, and (5) an eight-parameter regional model (model 5) where separate stock–recruitment curves were fit to density estimates for a different grouping of western, southern, eastern, and northern spatial units (Figure 2). Our initial findings suggested that a reduced (five-parameter regional model) version of model 4 (eight-parameter regional model) with single α and separate β parameters for western, southern, eastern, and northern spatial units (model 6) was more appropriate for describing age-1 cisco recruitment dynamics in Lake Superior than a priori models, so nonlinear regression (SYSTAT 2004) was used to estimate parameters for one post hoc model, i.e.,

$$\log_e(R_i/S_i) = \log_e(\alpha) - \beta_1 S_{i1} - \beta_2 S_{i2} - \dots - \beta_4 S_{i4} + \varepsilon,$$

where S_{i1} through S_{i4} are region-specific estimates of spawning stock size, and β_1 through β_4 are region-specific estimates of β.

The most parsimonious model describing age-1 cisco recruitment dynamics in Lake Superior was selected from the set of candidate models using Akaike's information criterion (AIC) and likelihood statistics (Anderson et al. 2000; Burnham and Anderson 2002):

$$AIC = n \log_e\left(\frac{RSS}{n}\right) + 2K,$$

where n is the number of data points used in model construction, RSS is the residual sum of squares for each model, and K is the number of parameters estimated for each model (Burnham and Anderson 2002). Because the number of data points used in model construction was low compared with the number of model parameters ($n/K \leq 40$) for most (four of six) models, a second-order modification of the AIC statistic (AIC_c) was used
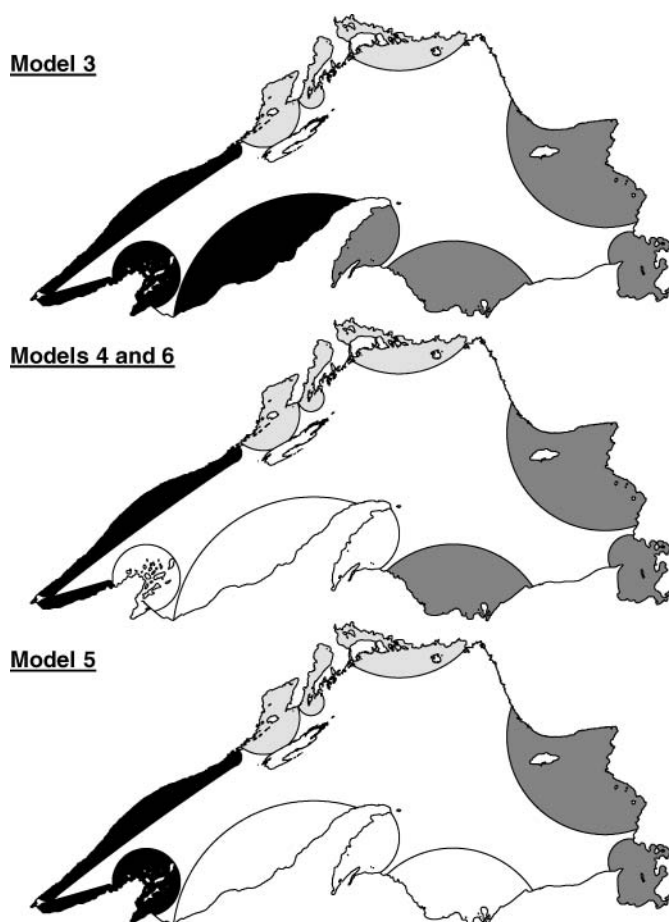

FIGURE 2. Regional spatial unit groupings for model 3, models 4 and 6, and model 5. Like colors represent regional groupings for each model. Separate stock–recruitment curves were fitted to density estimates for each group of spatial units. Model 6 (five-parameter regional model) was a reduced version of model 4 (eight-parameter regional model) with a single α and separate β parameters for each region. The top-ranked model selected by Akaike's Information Criterion (AIC) and likelihood statistics was model 6. Regions identified for modeling (as measured at the widest point) were 230 km (Minnesota and WI-1), 240 km (WI-2, Western Keweenaw, and MI-4), 270 km (Michigan South Shore, Whitefish Bay, and Eastern Canada), and 290 km (Nipigon Bay, Black Bay, and Thunder Bay).

for model ranking (Burnham and Anderson 2002), i.e.,

$$AIC_c = AIC + \frac{2K(K+1)}{n - K - 1}.$$

All models were ranked relative to the most parsimonious model (lowest AIC_c value) based on scaled AIC_c values (ΔAIC_c), which were calculated as the difference between the lowest AIC_c value ($AIC_{c\ min}$) and AIC_c values of other models. Akaike weights (w_i) were calculated to determine the weight of evidence in favor of each model (Burnham and Anderson 2002).

For the most parsimonious model describing age-1 cisco recruitment dynamics in Lake Superior, peak recruitment (R_{max}) and the spawning stock size that produced peak recruitment (S_{max}) were estimated for each region to show how cisco

TABLE 1. Summary statistics for estimated recruit densities used in model construction. Number of years used in model construction (*n*); average (Avg.), minimum (Min.), and maximum (Max.) recruit densities; average coefficient of variation (Avg. CV); and average relative standard error (Avg. RSE) are provided for each spatial unit (see Figure 1 for spatial unit abbreviations).

Spatial unit	*n*	Recruit density bottom trawls (fish/ha)				
		Avg.	Min.	Max.	Avg. CV	Avg. RSE
MINN	22	1.1	0.2	14.8	2.67	0.89
WI-1	14	11.2	0.2	45.9	110.31	62.24
WI-2	28	38.1	0.2	431.3	3.07	0.94
WKEW	16	3.1	0.2	22.9	5.29	2.63
MI-4	26	11.9	0.2	206.5	8.73	4.07
MISS	20	4.8	0.2	63.1	5.79	2.44
WFBY	11	0.4	0.2	1.5	1.65	0.75
ECAN	12	1.6	0.2	15.1	1.43	0.47
NIPB	17	2.1	0.2	10.2	5.68	2.15
BLKB	17	1.4	0.2	7.0	42.49	21.25
THBY	17	4.6	0.2	40.0	15.40	6.93

recruitment differed among regions. Peak recruitment was estimated as

$$R_{\max} = \frac{\alpha}{\beta e},$$

where α and β are parameters estimated from the Ricker stock–recruitment model (Ricker 1975; Hilborn and Walters 1992). The spawning stock size that produced peak recruitment was estimated as

$$S_{\max} = \frac{1}{\beta},$$

where β is the density-dependent parameter estimated from the Ricker stock–recruitment model (Ricker 1975; Hilborn and Walters 1992).

RESULTS

Spawner and Recruit Density

In years used for model construction, estimates of recruit density varied 102-fold in Minnesota, 197-fold in WI-1, 2,975-fold in WI-2, 158-fold in Western Keweenaw, 1,424-fold in MI-4, 435-fold in Michigan South Shore, 10-fold in Whitefish Bay, 104-fold in Eastern Canada, 71-fold in Nipigon Bay, 48-fold in Black Bay, and 276-fold in Thunder Bay. Average recruit density was greatest in WI-2 (38.1 fish/ha), followed by MI-4 (11.9 fish/ha), WI-1 (11.2 fish/ha), Michigan South Shore (4.8 fish/ha), Thunder Bay (4.6 fish/ha), Western Keweenaw (3.1 fish/ha), Nipigon Bay (2.1 fish/ha), Eastern Canada (1.6 fish/ha), Black Bay (1.4 fish/ha), Minnesota (1.1 fish/ha), and Whitefish Bay (0.4 fish/ha; Table 1). Lake-wide recruitment events occurred in 1984, 1988–1990, 1998, and 2003. However, relative year-class strength during lakewide recruitment events was highly variable among spatial units (Figure 3).

In years used for model construction, estimates of spawner density varied 1.2-fold in Minnesota, 120-fold in WI-1, 51-fold in WI-2, 19-fold in Western Keweenaw, 94-fold in MI-4, 6-fold in Michigan South Shore, 8-fold in Whitefish Bay, 5-fold in Eastern Canada, 7-fold in Nipigon Bay, 17-fold in Black Bay, and 28-fold in Thunder Bay. Average spawner density was greatest in WI-1 (8.6 fish/ha), followed by MI-4 (3.4 fish/ha), WI-2 (1.9 fish/ha), Thunder Bay (1.2 fish/ha), Black Bay (1.2 fish/ha), Nipigon Bay (0.5 fish/ha), Western Keweenaw (0.5 fish/ha), Whitefish Bay (0.5 fish/ha), Eastern Canada (0.4 fish/ha), Michigan South Shore (0.4 fish/ha), and Minnesota (0.2 fish/ha; Table 2). Spawner densities were generally low prior to 1988, increased during 1988–1997, and decreased after 1997 (Figure 4).

TABLE 2. Summary statistics for estimated spawner densities used in model construction. Number of years used in model construction (*n*); average (Avg.), minimum (Min.), and maximum (Max.) spawner densities; average coefficient of variation (Avg. CV trawls) and relative standard error (Avg. RSE) for bottom trawl density; and average coefficient of variation (Avg. CV) and relative standard error (Avg. RSE) for gill-net catch per unit effort (CPUE) are provided for each spatial unit (see Figure 1 for spatial unit abbreviations).

| Spatial unit	*n*	Spawner density (fish/ha)						
		Avg.	Min.	Max.	Avg. CV trawls	Avg. RSE trawls	Avg. CV gill-net CPUE	Avg. RSE gill-net CPUE
MINN	22	0.2	0.2	0.2	0.36	0.13	1.24	0.36
WI-1	14	8.6	0.3	36.2	19.59	10.43	2.42	0.49
WI-2	28	1.9	0.2	8.1	4.30	1.31	1.86	0.27
WKEW	16	0.5	0.2	2.7	2.39	0.96	1.94	0.56
MI-4	26	3.4	0.2	13.7	13.00	5.05	2.14	0.76
MISS	20	0.4	0.2	0.9	6.64	2.71	2.36	0.83
WFBY	11	0.5	0.2	1.2	2.50	0.84	77.28	54.17
ECAN	12	0.4	0.2	0.7	3.16	0.99	111.76	78.68
NIPB	17	0.5	0.2	1.2	4.30	1.68	4.68	2.99
BLKB	17	1.2	0.2	3.8	9.31	4.66	1.20	0.15
THBY	17	1.2	0.2	4.0	11.97	5.42	0.82	0.14
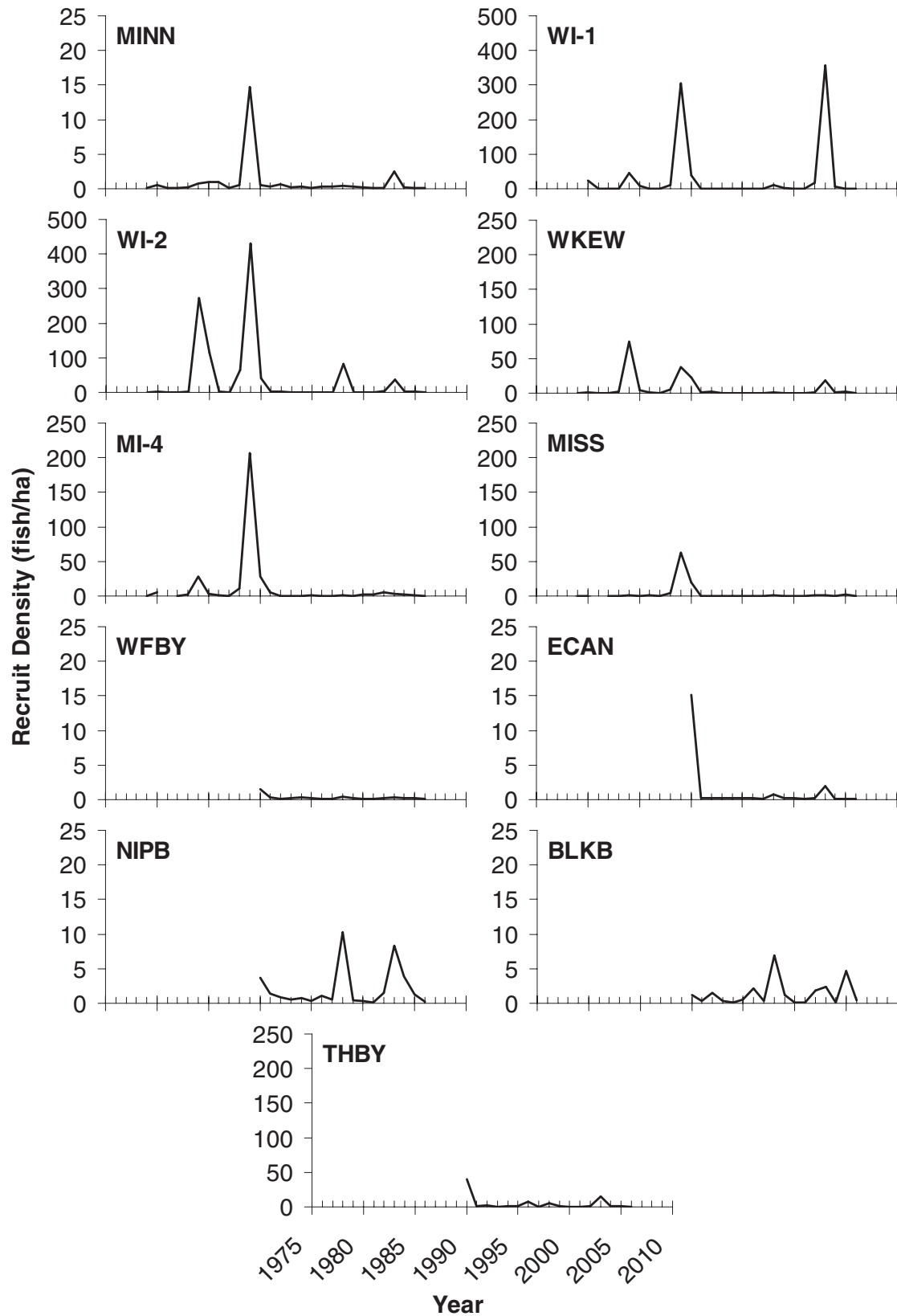
FIGURE 3. Geometric mean density of the 1979–2006 year-classes of ciscoes in Lake Superior. Years correspond to year of hatching. Density was indexed at age 1. Three different scales were used to represent high (0–500 fish/ha), medium (0–250 fish/ha), and low (0–25 fish/ha) density spatial units (see Figure 1 for spatial unit abbreviations). Densities displayed represent the full range of estimated densities and may include values not used in model construction.
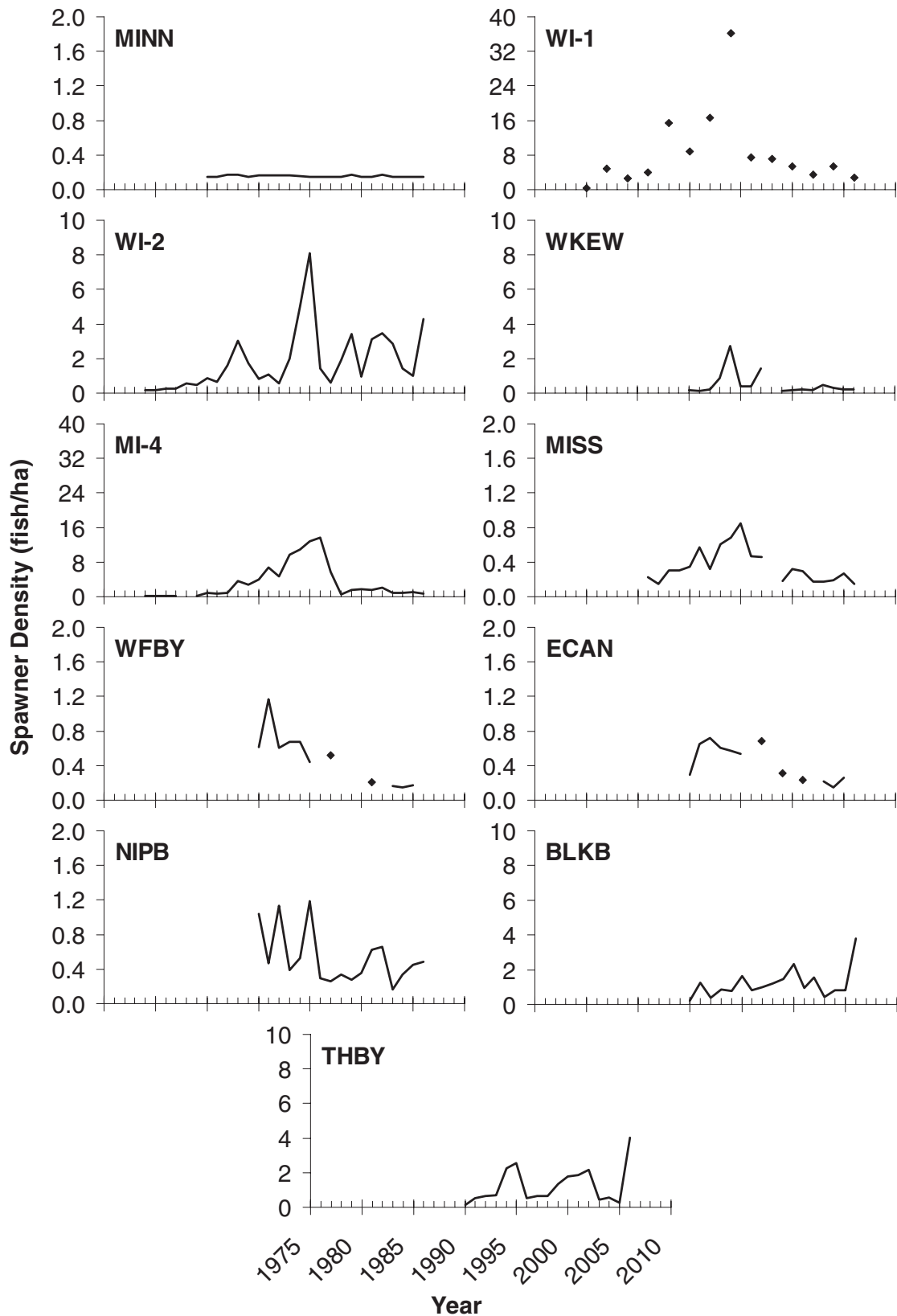
FIGURE 4.   Spawning stock sizes that produced the 1979–2006 year-classes of ciscoes in Lake Superior estimated using combined spring bottom-trawls and fishery-independent gill-net surveys or targeted commercial fisheries. Years provided correspond to year of hatching for year-classes produced during 1979–2006. Three different scales were used to represent high (0–40 fish/ha), medium (0–10 fish/ha), and low (0.0–2.0 fish/ha) density spatial units (see Figure 1 for spatial unit abbreviations). Densities displayed represent the full range of estimated densities and may include values not used in model construction.

TABLE 3. Comparison of Ricker stock–recruitment models describing age-1 cisco recruitment dynamics in Lake Superior. Models are ranked in order of scaled second-order Akaike information criterion (AIC_c) values. Akaike weights (w_i) can be interpreted as the probability that a given model is the correct model of all the models considered. The number of data points used in model construction (n) and the residual sum of squares for each model (RSS) are also provided. The top-ranked model (Model 6; highlighted) had an 85% likelihood of being the correct model, was 6.0-fold more likely than the second-ranked model, and was 5.8-fold more likely than all other models.

Model	n	Number of parameters	RSS	AIC	AIC_c	Scaled AIC_c	w_i
6	200	5	557.951	215.191	215.500	0.000	0.85
4	200	8	550.023	218.329	219.083	3.582	0.14
5	200	8	568.749	225.024	225.778	10.278	0.00
3	200	6	600.689	231.952	232.387	16.887	0.00
1	200	22	517.708	234.219	239.936	24.436	0.00
2	200	2	672.635	246.577	246.638	31.138	0.00

Spatial Scale

Recruitment variation of ciscoes in Lake Superior was best described by a five-parameter regional model (model 6) with a single α and separate β parameters for western, southern, eastern, and northern spatial units (Table 3). Regional spatial unit groupings included Minnesota and WI-1 as Region 1; WI-2, Western Keweenaw, and MI-4 as Region 2; Michigan South Shore, Whitefish Bay, and Eastern Canada as Region 3; and Nipigon Bay, Black Bay, and Thunder Bay as Region 4 (Figure 2). The four-group regional model had an 85% likelihood of being the correct model of all models considered, was 6.0-fold more likely than the second-ranked model, and was 5.8-fold more likely than all other models combined. The spatial scale for modeling was about 260 km (range = 230–290 km).

Model Parameters and Fit

The density-independent recruitment rate was constant among regions ($\alpha = 3.6$ age-1 recruits/spawner), whereas the rate of compensatory density dependence varied 16-fold among regions and was greatest in Region 3 ($\beta = -2.9$/spawner), followed by Region 4 ($\beta = -1.2$/spawner), Region 2 ($\beta = -0.4$/spawner), and Region 1 ($\beta = -0.2$/spawner; Table 4). Both peak recruitment (R_{max}) and the spawning stock size that produced peak recruitment (S_{max}) varied 16-fold among regions and were greatest in Region 1 ($R_{max} = 7.1$ age-1 recruits/ha and $S_{max} = 5.3$ spawners/ha), followed by Region 2 ($R_{max} = 3.0$ age-1 recruits/ha and $S_{max} = 2.3$ spawners/ha), Region 4

($R_{max} = 1.1$ age-1 recruits/ha and $S_{max} = 0.9$ spawners/ha), and Region 3 ($R_{max} = 0.5$ age-1 recruits/ha and $S_{max} = 0.3$ spawners/ha; Table 4; Figure 5). All four regional models were significant ($P \leq 0.05$). However, strong recruitment events were consistently underestimated (Figure 6). Adjusted R^2 values for linear models ranged from 0.22 to 0.37 (Table 4), and time series (Hilborn and Walters 1992) and normal probability (SYSTAT 2004) plots indicated that model residuals were independent and approximately normally distributed for all regions except Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada).

DISCUSSION

Our findings are consistent with previously observed regional differences in age-1 cisco year-class strength and regional deviations from normal patterns of recruitment synchrony (Ebener et al. 2008; Stockwell et al. 2009) and support the hypothesis that factors driving cisco recruitment operate within four different regions of Lake Superior. Previously, commercial fishery records were used to identify six major cisco spawning stocks (Selgeby 1982) and eight discrete cisco spawning stocks (Goodyear et al. 1981) in Wisconsin waters of Lake Superior. More recently, genetically discrete stocks were identified in Black Bay and Thunder Bay (K. T. Scribner, Michigan State University, personal communication). Therefore, regions identified in our study likely contain multiple spatially or genetically discrete cisco stocks.

TABLE 4. Comparison of regional (as defined in Figure 2) stock–recruitment curves based on the top-ranked model describing age-1 cisco recruitment dynamics in Lake Superior (see Figure 1 for spatial unit abbreviations). Estimated parameters (α and β) and asymptotic standard errors (ASE) are provided, along with peak recruitment (R_{max}), the spawning stock size that produced peak recruitment (S_{max}), and adjusted R^2 values for linear versions of the Ricker stock–recruitment model. Differences among regional models were driven by different levels of compensatory density dependence in each region.

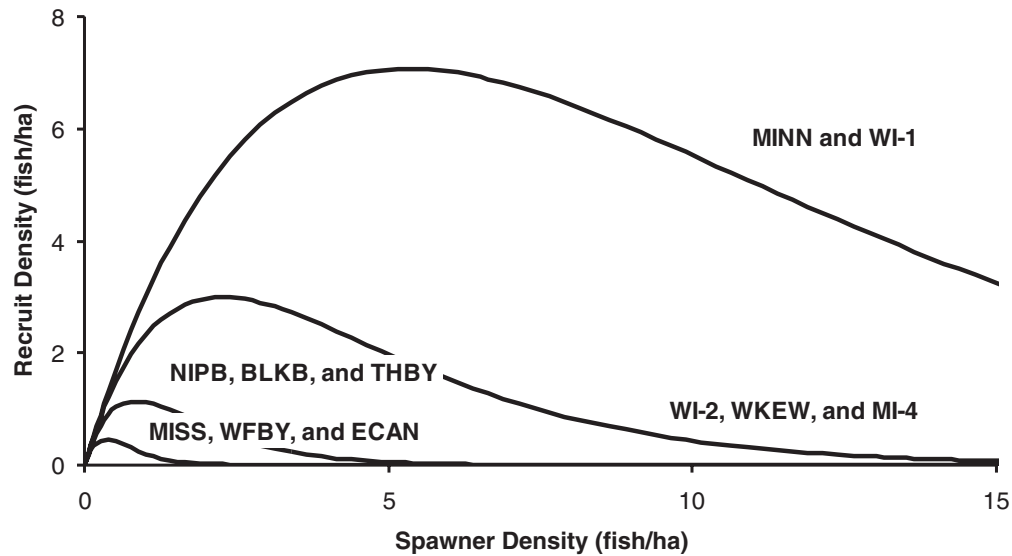| Region	α	ASE	β	ASE	R_{max}	S_{max}	Adjusted R^2 linear model	P-value
MINN and WI-1	3.6	0.59	−0.2	0.04	7.1	5.3	0.28	0.004
WI-2, WKEW, and MI-4	3.6	0.59	−0.4	0.06	3.0	2.3	0.29	<0.001
MISS, WFBY, and ECAN	3.6	0.59	−2.9	0.62	0.5	0.3	0.22	<0.001
NIPB, BLKB, and THBY	3.6	0.59	−1.2	0.21	1.1	0.9	0.37	<0.001

FIGURE 5.   Comparison of nonlinear regional (as defined in Figure 2) stock–recruitment curves based on the top-ranked model describing age-1 cisco recruitment dynamics in Lake Superior. Differences among regional models were driven by different levels of compensatory density dependence in each region (see Figure 1 for spatial unit abbreviations).
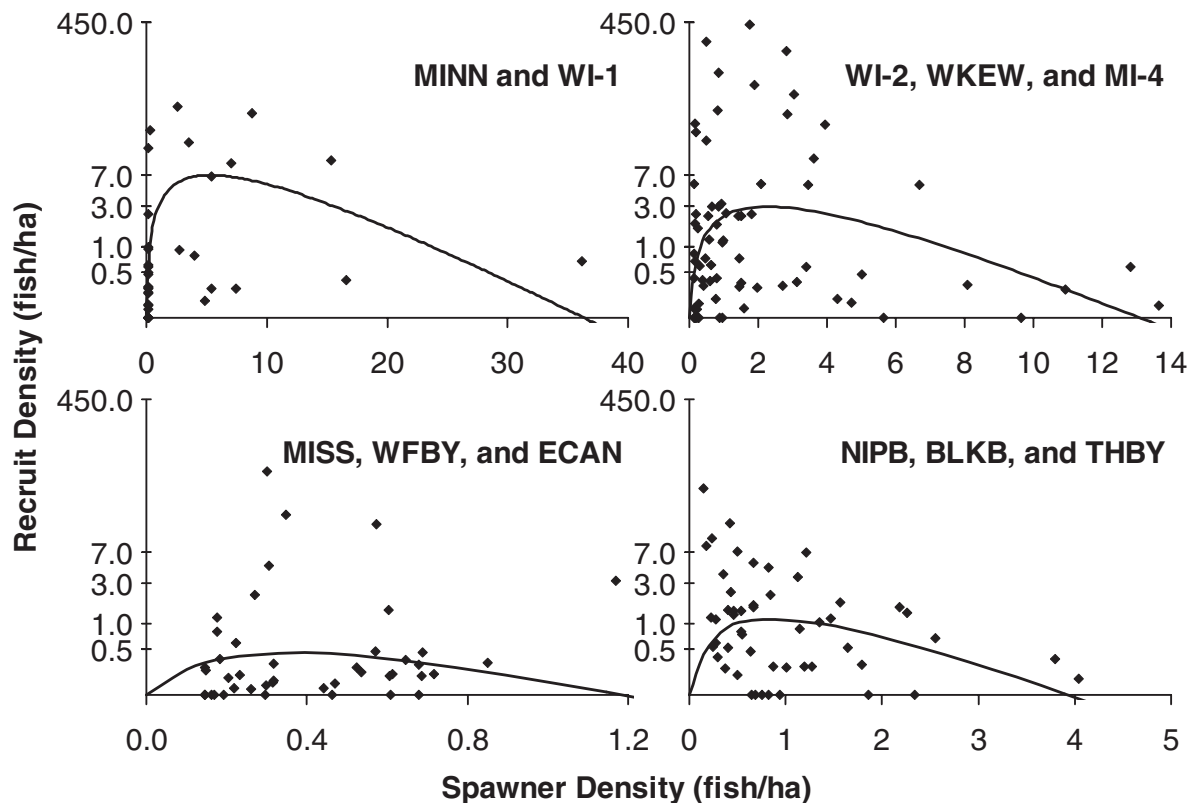

FIGURE 6.   Comparison of nonlinear regional (as defined in Figure 2) stock–recruitment curves based on the top-ranked model describing age-1 cisco recruitment dynamics in Lake Superior (see Figure 1 for spatial unit abbreviations). Points are observed values and lines are predicted values. Recruit densities are plotted on a modified $\log_e$ scale to allow both observed and predicted values to be displayed. Strong recruitment events were consistently underestimated.

The spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior was 16-fold larger than the average movement distance (16.5 km; weighted average calculated from reported data) and 3-fold larger than the maximum movement distance (88.5 km) reported for ciscoes in Lake Michigan (Smith and Van Oosten 1940), which suggests that large-scale abiotic factors (i.e., "climate forcing" or the "Moran Effect"; Koenig 2002; Bronte et al. 2003; Engen and Saether 2005; Phelps et al. 2008; Gorman and Hoff 2009) are more important than small-scale biotic factors in influencing cisco recruitment in Lake Superior. Compared with the spatial scale of recruitment correlations for other fish species, the spatial scale for modeling was larger than for other freshwater species (<50 km), smaller than for marine species (about 500 km), and similar to anadromous species and species with estuarine nursery regions (50–500 km; Myers et al. 1995; Myers et al. 1997; Myers 2001), which suggests that the relative importance of large-scale abiotic factors in influencing cisco recruitment in Lake Superior is intermediate compared with other freshwater and marine species. Differences between the spatial scale for modeling and the spatial scale of recruitment correlations for other freshwater and marine species may be related to the size of Lake Superior (Lawrie and Rahrer 1973), which is intermediate compared with most freshwater and marine environments. The differences could also be related to the early life history characteristics of cisco in Lake Superior (Anderson and Smith 1971; Scott and Crossman 1973; Becker 1983; Selgeby et al. 1994; Oyadomari and Auer 2004), which are similar to marine species (i.e., have extended planktonic larval stages) and species with estuarine nursery regions. The relatively large size of Lake Superior may lead to relatively low fish densities similar to those found in marine environments, thereby creating a situation where the influence of small-scale biotic factors (e.g., predation and competition) is reduced and large-scale abiotic factors are allowed to exert greater influence on the recruitment process (see Myers et al. 1997 for a more complete discussion). The early life history characteristics of ciscoes in Lake Superior, which include a planktonic larval stage and dependence on nearshore rearing areas (Anderson and Smith 1971; Scott and Crossman 1973; Becker 1983; Selgeby et al. 1994; Oyadomari and Auer 2004), may make ciscoes highly susceptible to large-scale abiotic factors driving growth (Houde 1989; Hare and Cowen 1997; Oyadomari and Auer 2004), predator–prey encounter rates (McGurk 1986; MacKenzie and Leggett 1991; Hare and Cowen 1997; Hinrichsen et al. 2003; Hoff 2004), and larval retention or dispersal (Hare and Cowen 1996; Hare and Cowen 1997; Hinrichsen et al. 2003; Oyadomari and Auer 2004), thereby creating a situation more commonly experienced by marine species with extended planktonic larval stages and species with estuarine nursery regions. Further, because the life history strategy of ciscoes in Lake Superior can be considered a mix of both periodic (i.e., high fecundity, small egg size, and high gonado-somatic index; Scott and Crossman 1973; Becker 1983) and equilibrium (i.e., long-lived [up to 20 years or more]; Ebener et al. 2008; Stock-

well et al. 2009) strategies, the relative importance of large-scale abiotic factors in influencing recruitment may be intermediate compared with typical periodic and equilibrium species, thereby leading to intermediate spatial scales for recruitment synchrony and modeling (e.g., Tedesco and Hugueny 2006).

Previously, Hoff (2004) used a generalized version of the Ricker stock–recruitment model (Hilborn and Walters 1992), U.S. Geological Survey spring bottom-trawl survey data (described above), and multiple regression techniques (Zar 1999) to identify and quantify the effects of multiple biotic and abiotic factors correlated to age-1 cisco recruitment. Hoff (2004) estimated a density-independent recruitment rate of 5.4 age-1 recruits/spawner and a rate of compensatory density dependence of −0.3/spawner for ciscoes in Wisconsin waters of Lake Superior (based on the reported single-factor model; Hoff 2004). The previously reported density-independent recruitment rate was 1.5-fold greater than the rate in our study but within the range of estimation errors, which suggests that parameter estimates did not differ substantially between our study and Hoff (2004). In contrast, the previously reported rate of compensatory density dependence was similar to rates in the western and southern regions of our study and within the range of estimation errors but lower than the rates in our study and outside the range of estimation errors in the eastern and northern regions, which suggests that parameter estimates differed substantially between our study and Hoff (2004) in two of four regions. The constant density-independent recruitment rate among regions in our study and between our study and Hoff (2004) is consistent with previous studies (Myers et al. 1996; Myers et al. 1999) that found relatively constant within-species maximum annual reproductive rates for multiple freshwater and marine fish stocks, which suggests that the ability to reproduce at low spawning stock size may be genetically predetermined and similar for cisco stocks throughout Lake Superior. Highly variable rates of compensatory density dependence among regions in our study and between our study and Hoff (2004) suggest that regional deviations from normal patterns of recruitment synchrony in Lake Superior (Ebener et al. 2008; Stockwell et al. 2009) are driven by regional differences in compensatory density dependence, such as egg predation (Dryer and Beil 1964; Anderson and Smith 1971; Becker 1983), larval predation (Pritchard 1931; Becker 1983; Hoff et al. 1997a), or competition during the first year of life (Selgeby et al. 1978; Rudstam et al. 1993; Link et al. 1995; Jensen 1996; Kinnunen 1997; Pangle et al. 2004). Therefore, large-scale abiotic factors may drive age-1 cisco recruitment in Lake Superior at spatial scales greater than those identified for modeling (e.g., lakewide scale), whereas small-scale biotic factors drive recruitment within each region.

Estimates of peak recruitment and the spawning stock size that produced peak recruitment in our study were consistently lower than previous estimates for ciscoes in Lake Superior, varied among regions, and were greatest for the most productive (western and southern) and lowest for the least productive (eastern and northern) regions. Peak recruitment was lower than a

previous estimate for ciscoes in Wisconsin waters of Lake Superior (8.0 age-1 recruits/ha, based on the reported single-factor model; Hoff 2004) in all four regions, varied 16-fold among regions, and was 6-fold greater in western and southern regions than eastern and northern regions. Similarly, the spawning stock size that produced peak recruitment was lower than a previous estimate for ciscoes in Wisconsin waters of Lake Superior (4.0 spawners/ha, based on the reported single-factor model; Hoff 2004) in three of four regions, varied 16-fold among regions, and was 6-fold greater in western and southern regions than eastern and northern regions. Consistently lower estimates of peak recruitment and the spawning stock size that produced peak recruitment in our study suggest that differences between our study and the previous study may be related to systematic differences in the data analyzed (e.g., spatial, temporal, or two different methods used to index adult spawning stock size). Regional differences in peak recruitment and the spawning stock size that produced peak recruitment in our study suggest that regional carrying capacity related to productivity or the total area of suitable rearing habitat (e.g., Myers et al. 2001) may be an important underlying factor driving regional differences in age-1 cisco recruitment throughout Lake Superior.

We used single-factor stock–recruitment models to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior, but consistent underestimation of strong recruitment events, low adjusted R^2 values for all four linear models, and nonnormally distributed model residuals for Region 3 suggest that one or more important variables may be missing from each regional model. Further, regional differences in peak recruitment and the spawning stock size that produced peak recruitment in our study suggest that regional carrying capacity related to productivity or the total area of suitable rearing habitat may be an important underlying factor driving regional differences in age-1 cisco recruitment throughout Lake Superior. Therefore, future studies of cisco stock–recruitment in Lake Superior should focus on evaluating potential regional differences in carrying capacity and developing multi-factor stock–recruitment models. To evaluate potential regional differences in carrying capacity, researchers should consider weighting indices of recruitment and adult spawning stock size by the total area of suitable rearing habitat within units used for analyses (e.g., spatial units in this study). Weighting population indices by the total area of suitable rearing habitat effectively removes habitat area as a confounding factor in calculating the rate of compensatory density dependence and allows management parameters estimated from regional stock–recruitment models (i.e., peak recruitment and the spawning stock size that produced peak recruitment) to be directly compared in terms of productivity (Myers et al. 2001). However, weighting population indices by the total area of suitable rearing habitat may substantially alter modeling results compared with results based on nonweighted population indices (e.g., different regional spatial unit groupings in this study). Therefore, potential differences in carrying capacity should be evaluated prior to any multi-factor modeling. Adding multiple biotic and abiotic factors to stock–recruitment models may help researchers identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics in Lake Superior, generate hypotheses that can be tested in future laboratory and field studies, and substantially improve model fit. Candidate variables for multifactor models should include variables previously correlated to, or generally considered to regulate age-1 cisco recruitment in Lake Superior, as well as variables previously correlated to recruitment of other coregonid species in the Great Lakes. Potential variables include (1) air temperature, biomass of slimy sculpin *Cottus cognatus*, and lake trout abundance (Hoff 2004), (2) rainbow smelt *Osmerus mordax* abundance (Anderson and Smith 1971; Walter and Hoagman 1975; Selgeby et al. 1978; Hrabik et al. 1998; Cox and Kitchell 2004; Gorman 2007, 2012), (3) bloater *Coregonus hoyi* abundance (Anderson and Smith 1971; Davis and Todd 1992), (4) abundance of other cisco age-classes (Jensen 1996; Bronte et al. 2003; Hoff 2004; Gorman and Hoff 2009), and (5) ice cover (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993). The spatial scale identified for modeling in our study suggests that abiotic factors capable of influencing the recruitment process at spatial scales greater than 200–300 km (e.g., wind speed, air temperature, and ice cover) may provide the greatest improvements in model fit when added to stock–recruitment models. However, biotic factors capable of influencing the recruitment process at much smaller spatial scales (e.g., <200–300 km) will likely be required to account for additional residual variation not explained by abiotic factors (e.g., Madenjian et al. 1996; Hansen et al. 1998, and Hoff 2004).

MANAGEMENT IMPLICATIONS

Previously, studies of cisco stock–recruitment in the Great Lakes were limited to one study of cisco stock–recruitment in Wisconsin waters of Lake Superior (Hoff 2004). The previous study used a multifactor modeling approach (described above) to identify and quantify the effects of biotic and abiotic factors correlated to age-1 cisco recruitment but failed to identify or quantify the spatial scale for cisco recruitment dynamics and management parameters estimated for cisco stocks in Wisconsin waters of Lake Superior were not broadly applicable to cisco stocks in other regions of Lake Superior or the lower Great Lakes. Our findings provide the first estimate of the spatial scale for cisco recruitment dynamics and the first comprehensive estimates of basic management parameters for cisco stocks in the Great Lakes. However, consistent underestimation of strong recruitment events and relatively poor model fit suggest that future multifactor modeling efforts will be needed before basic management parameters estimated in our study can be more broadly applied. Further, we did not use weighted indices of recruitment and adult spawning stock size to evaluate potential regional differences in carrying capacity related to productivity or the total area of suitable rearing habitat. Therefore, we suggest that our results should only be used as part of a general conceptual

framework to guide cisco restoration and management efforts throughout Lake Superior and the lower Great Lakes.

We suggest that fishery managers throughout Lake Superior and the entire Great Lakes basin should address cisco restoration and management efforts on a regional scale in each lake and that regions targeted for cisco restoration and management efforts should range from 200 to 300 km (measured at the widest point). Based on previous studies of cisco stock structure in Lake Superior (Goodyear et al. 1981; Selgeby 1982; K. T. Scribner, Michigan State University, personal communication) and cisco movement in Lake Michigan (Smith and Van Oosten 1940), regions identified for modeling in our study likely contain multiple spatially or genetically discrete cisco stocks. Therefore, management of cisco fisheries on a stock-by-stock or management unit-by-management-unit basis (see Ebener et al. 2008 and Stockwell et al. 2009) will be required, with the understanding that large-scale abiotic factors influencing the stock–recruitment process on a regional (or larger) scale (e.g., >200–300 km) likely drive recruitment patterns of multiple spatially or genetically discrete cisco stocks. These spatially or genetically discrete cisco stocks are then influenced by biotic factors acting on the recruitment process at much smaller spatial scales (e.g., <200–300 km).

Our findings suggest that cisco spawning stock size should be maintained near densities of 5.3 spawners/ha in western spatial units, 2.3 spawners/ha in southern spatial units, 0.3 spawners/ha in eastern spatial units, and 0.9 spawners/ha in northern spatial units to produce peak recruitment of age-1 ciscoes in Lake Superior. However, because parameter estimates will likely change with the use of weighted population indices (e.g., Myers et al. 2001) and the addition of multiple explanatory variables (e.g., Madenjian et al. 1996; Hansen et al. 1998, and Hoff 2004), fishery managers should exercise caution when applying management parameters estimated in our study to cisco populations throughout Lake Superior. Similarly, estimates of the spawning stock size that produced peak recruitment of age-1 cisco in Lake Superior can be used as targets for the restoration of remnant cisco populations throughout the lower Great Lakes. However, because the productivity and trophic-community structure of Lake Superior differs from many of the lower Great Lakes, fishery managers should exercise caution when applying management parameters estimated in our study to the lower Great Lakes. Because of Lake Superior's low productivity (Hansen 1990; Horns 2003), fishery managers should consider regional estimates of the spawning stock size that produced peak recruitment of age-1 cisco in Lake Superior as minimum targets for the restoration of cisco populations throughout the lower Great Lakes. However, because the trophic-community structure of the lower Great Lakes is dominated by invasive species, such as the alewife, dreissenid mussels, and the exotic zooplankter *Bythotrephes* (Mills et al. 2003; Dobiesz et al. 2005; Nalepa et al. 2009; Fahnenstiel et al. 2010), which have altered zooplankton community structure and abundance (Mills et al. 2003; Dobiesz et al. 2005), the capacity of the lower Great Lakes to sustain historical cisco densities may be greatly reduced, especially in nearshore waters (Johannsson et al. 2000; Mills et al. 2003). Current reductions in alewife abundance throughout the lower Great Lakes (O'Gorman and Stewart 1999) may provide an opportunity to reestablish historical cisco populations and provide a more stable, long-lived, and locally adapted forage base than exists in current communities dominated by invasive species (Fitzsimons and O'Gorman 2006). However, a high degree of uncertainty regarding target densities for cisco restoration and the long-term sustainability of the species throughout the lower Great Lakes will likely persist into the future (Hoff 2004; Fitzsimons and O'Gorman 2006; Ebener et al. 2008; Stockwell et al. 2009; Zimmerman and Krueger 2009).

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